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Dietz, M.W.; Drent, R.H.

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Effect of Growth Rate and Body Mass on Resting Metabolic Rate in Galliform Chicks

Maurine W. Dietz[1,2,*]
Rudi H. Drent[2]
[1]Department of Veterinary Basic Sciences, Division of Physiology, University of Utrecht, 3508 TD Utrecht, The Netherlands; [2]Centre for Ecological and Evolutionary Studies, Zoological Laboratory, University of Groningen, 9750 AA Haren, The Netherlands

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ABSTRACT

In this study, we asked whether within-species variation in chick resting metabolic rate was related to variation in growth and whether this relationship changed during development in three galliform species (turkey, *Meleagris gallopavo*, guinea fowl, *Numida meleagris*, and Japanese quail, *Coturnix coturnix japonica*). Resting metabolic rate increased by a bi- or triphasic pattern with body mass. For each phase, the relationship between metabolic rate and growth was studied by residual analysis, with two measures of growth: growth rate and body mass. Chick mass reflects the net result of accumulated growth, while hatchling mass reflects embryonic growth. In hatchlings, high metabolic rates coincided with low growth rates in turkeys and guinea fowl. These species delay initial food intake, and under these circumstances high metabolic expenditure may preclude conversion of yolk energy into body mass. No relationship was present between residual hatchling metabolic rate and residual body mass. In older chicks, residual metabolic rate was positively linearly related with residual growth rate (turkeys and young quail) or residual body mass (guinea fowl and older quail). The similarity of the slopes suggests that growth rate and accumulated growth affected maintenance metabolism to the same extent throughout development. These findings suggest that growth models must take ontogenetic adjustments of metabolic rate into account in addition to costs of maintenance.

Introduction

Maintenance and growth costs are important components of the total costs of development in growing chicks (Ricklefs and White 1981; Williams and Prints 1986; Drent and Klaassen 1989). In tern and gull chicks, maintenance accounts for about 45% of the total energy budget during the nestling period, while the energy used for the production of body tissue makes up about 27% of the total energy budget (Drent et al. 1992). A point of interest in estimating chick energy budgets is the effect of variation in growth rate on the total energy cost of development. In his review, Ricklefs (1983) concluded that the effect of increasing relative growth rate (assuming constant asymptotic body mass) on the energy budget is small; in one calculated example, a doubling of the relative growth rate would increase the maximum energy requirements by only 20%.

However, as Drent and Klaassen (1989) pointed out, Ricklefs's calculations depend on the assumption that the maintenance costs are unaffected by growth rate. In an interspecific comparison within three family groups (Laridae; Procellariidae; and Charadriidae, Scolopacidae, and Haematopidae), they showed that resting metabolic rate (RMR) of hatchlings in the thermoneutral zone was positively correlated with the average relative growth rate during posthatch development (Drent and Klaassen 1989; Klaassen and Drent 1991). According to their analysis, a doubling of the growth rate would result in a 40% increase of hatchling RMR. Extrapolating this finding to older chicks, Drent and Klaassen (1989) calculated that at the inflection point a doubling of the average relative growth rate would result in a 63% increase of the daily energy costs. In older chicks, the variation in RMR is also related to the variation in growth, as Klaassen and Bech (1992) have shown in Arctic tern chicks (*Sterna paradisea*). In their study, they measured growth as the deviation of the body mass from the general growth curve for the species, assuming that body mass presents the net effect of previous or accumulated growth of a chick up to a particular age.

As in adult basal metabolic rate, chick RMR is strongly correlated with body mass, although in chicks this relationship is not a simple allometric linear regression. In contrast to adult basal metabolic rate, chick RMR includes also other costs, such as costs of digestion, assimilation, processing and storage (i.e., specific dynamic action), and growth (i.e., biosynthesis). In most precocial chicks, RMR increases with body mass by a bi- or triphasic allometric linear pattern (Weathers and Siegel 1995; Weathers 1996). The physiological basis for this developmental pattern is not fully known; the increasing mass and function of the digestive system and the increase in functional maturity of the metabolically active tissues may be responsible (Grav et al. 1988; Kroghdahl and Sell 1989; Choi et al. 1993;

*To whom correspondence should be addressed; Centre for Ecological and Evolutionary Studies, Zoological Laboratory, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands. E-mail: m.w.dietz@biol.rug.nl.

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Nir et al. 1993; Dietz 1995; Weathers and Siegel 1995). The multiphasic development of RMR with body mass suggests that physiological relationships, such as between RMR and growth, may differ between different phases of development and should be assessed for the phases separately.

In this study, we asked whether within-species variation in RMR was related to variation in growth and whether this relationship changed during development in three galliform species (turkey, *Meleagris gallopavo,* guinea fowl, *Numida meleagris,* and Japanese quail, *Coturnix coturnix japonica*). The metabolic machinery of the chicks may be adapted to past growth, as assumed by Klaassen and Bech (1992), but also to present growth or future growth (Drent and Klaassen 1989; Klaassen and Drent 1991). Therefore, we took two measures of growth into account: present growth, that is, actual growth rate and past growth, represented by body mass.

Material and Methods

Animals and Housing

Fresh eggs of turkey (strain: B.U.T. Big 6), guinea fowl (strain: Galor), and Japanese quail (meat type) were obtained from commercial breeders and incubated at the Utrecht laboratory in accordance with the standard practice for each species (for methods see Dietz [1995]). The eggs were put into the incubator in three batches on subsequent days, so that chicks hatched on at least 3 subsequent days. Hatchlings were marked and weighed (±0.01 g) after drying at about 1–2 h after hatching and were kept up to 8–12 h posthatch in the incubator (37.5°C). Turkey and guinea fowl chicks were housed on a litter floor inside a temperature-controlled room with a light-dark cycle of 23L : 1D (dark: 5:00–6:00 A.M.); these are standard rearing conditions in the poultry industry. Water and commercial food were available ad lib. Quail chicks were housed in cages with mesh wire floors placed inside a temperature-controlled room under the same conditions as turkeys and guinea fowl chicks.

All chicks were weighed daily during the first 14 d posthatch (±0.1 g); thereafter, the weighing frequency decreased from two to three times a week to once a week. We were unable to determine the sex of hatchlings by cloacal examination, and initially the sexes were indistinguishable. At the end of the experiments, all birds were killed, and they were sexed by visual inspection of the gonads.

Metabolic Rate

Before a trial, the chicks had free access to food and water. Individual chicks were placed in a darkened metabolic chamber on a mesh wire floor. Chamber size was adjusted to chick size and ranged from 0.43 L for quail hatchlings (chamber was aluminum with glass lid) to 258 L for adult turkeys (chambers were galvanized drums). The ambient temperature inside the metabolic chamber (±0.1°C) was kept constant and monitored during the trial. Dry outdoor air was pulled in through the chamber. Flow rates of the outlet air, measured with a wet precision gas meter, were adjusted to maintain the O_2 consumption ($\dot{V}O_2$) and CO_2 production ($\dot{V}CO_2$) at around 0.5% and varied between about 0.08 L min^{-1} (STPD) for quail hatchlings and about 31.5 L min^{-1} (STPD) for adult turkeys. The outlet air was dried (molecular sieve 3 Å, Merck) before measuring O_2 and CO_2 concentrations. The O_2 and CO_2 analyzers (Taylor Servomex OA 184 O_2 analyzer and Leybold Heraeus Binos CO_2 analyzer) were calibrated each experimental day with pure N_2 and a calibrated gas mixture (consisting of N_2, O_2, and CO_2). The O_2 and CO_2 concentrations of the inlet air were measured at regular intervals.

After an equilibration period of 30 min, O_2 and CO_2 concentrations of the outlet air were measured continuously for a further 30 min. A stable registration of at least 15 min near the end of the 1-h trial was used to calculate average metabolic rate (MR, W) as $MR = 4.49\ \dot{V}O_2 + 1.39\ \dot{V}CO_2$, where $\dot{V}O_2$ and $\dot{V}CO_2$ were measured in liters per hour (STPD) (Romijn and Lokhorst 1961). Before calculating MR, the O_2 concentrations of the outlet air were corrected for the differences in volume of the inlet and outlet air at respiratory quotients below 1 (Hill 1972). After the trial, the chick was weighed (±0.1 g).

Measurements were done at a minimum of six different ambient temperatures per age. The temperature range varied with age and species, ranging from about 20.0°–42.5°C in hatchlings to about −9.0° to 35.0°C in adults. For each age the thermoneutral zone was estimated, and the measurements within the thermoneutral zone represented individual RMRs. In very young chicks, the thermoneutral zone was extremely narrow and could be determined only as one single point, the comfort temperature (the thermoneutral zone was defined as the 95% confidence interval around this comfort temperature). In chicks older than 48 d, the increase in MR with decreasing temperatures was small. Because of technical limitations, these chicks could not be exposed to very low temperatures, and the overall temperature range below the lower critical temperature was relatively narrow. Although it was difficult to determine the thermoneutral zone in chicks older than 48 d precisely, the temperature range with the lowest level of RMR was assumed to equal the thermoneutral zone.

Ages at which measurements were performed varied with species, to obtain an even distribution of the data along the logarithmic body mass range. Measurements were made at days 0 (i.e., 10–24 h posthatch), 3, 6, 11, 20, 27, 48, 69, 91, 132, and 233 in turkeys; at days 0 (i.e., 10–24 h posthatch), 3, 6, 10, 15, 27, 35, 48, 69, 103, and 159 in guinea fowl; and at days 0 (i.e., 10–24 h posthatch), 3, 6, 9, 13, 21, 27, 34, 48, and 63 in Japanese quail. At each age, chicks were randomly assigned to the different temperatures. In general, the chicks were subjected to a respirometry trial once or twice a day, but never more than three times a day and usually not at consecutive ages. The recovery time between trials was at least 2 h, to allow

the chicks to restore their body temperature to normal values, which was checked by routine cloacal body temperature measurements immediately before and after a trail (calibrated thermistor probe Therm 2236-1, ±0.1°C). During the recovery time, the chicks had free excess to food and water. In total, 67 turkey, 71 guinea fowl, and 91 quail chicks were used in the experiments.

Growth

We used two measures of growth, actual absolute growth rate and body mass. Absolute growth rate (g d^{-1}) was estimated for individual chicks at the ages at which RMR was determined, using the body masses of the chicks measured before and after the trial. Thus, absolute growth rate at trial *X* was calculated from the difference in body mass and time between the weighings before and after trial *X*. The time period between the weighings ranged from 1 d in very young chicks to 7 d in older chicks.

We assume that the body mass reflects the past, accumulated growth of a chick. Note that this assumption may be invalid in chicks with an irregular feeding pattern, in which the body mass of a chick may vary with time elapsed since food intake. The body mass (g) of a chick at trial *X* was used to estimate the variation in accumulated growth at trial *X* by calculating the deviation of mass from the general growth curve. For hatchlings, a modified procedure is called for, as past growth in this case refers to growth in the egg. The embryonic growth curve was used to estimate variation in the accumulated growth of hatchlings. Embryonic masses, determined in another experiment (Dietz 1995), were used to calculate embryonic growth curves. In that experiment, four eggs of average egg mass (±5%; accuracy, 0.1 mg) and of average eggshell water vapor conductance (±15%; accuracy, 0.1 mg d^{-1} $Torr^{-1}$; for methods see Tullet [1981]) were opened every 1–2 d from about day 7 of incubation onward. After opening the egg, the embryo was separated from the membranes and yolk and blotted dry before weighing to the nearest 0.1 mg.

Statistics

A continuous multiphasic linear regression model (Koops and Grossman 1993; Kwakkel et al. 1993) was applied to estimate the thermoneutral zone and to describe the multiphasic allometric relationship between RMR and body mass. This model has been designed to circumvent the problems besetting fit-by-eye or discontinuous analysis of linear segments, such as encountered by Freeman (1967). The results of a biphasic analysis with the model are consistent with results of the continuous two-phase model described by Nickerson et al. (1989). The general model is

$$Y = a + b_i X - \sum_{i=1}^{n-1} [r(b_i - b_{i+1})\ln(1 + e^{(X-c_i)/r})],$$

where Y is the dependent variable, a is the intercept, b_i is the slope of phase i, X is the independent variable, n is the number of phases, c_i is the estimated breakpoint between phase i and $i + 1$, and r is a smoothness parameter that was set at 0.05, a rather abrupt transition (Koops and Grossman 1993). All curves were fitted according to the nonlinear regression algorithm procedures from the NONLIN package (shareware program, P. H. Sherrod). The significance of adding an additional phase to the model was assessed by an *F*-test to verify the multiphasic nature of the relationship (Kwakkel et al. 1993).

Gompertz growth curves were fitted through the individual body masses at the experimental ages with the NONLIN package, according to the formula:

$$m(t) = Ae^{-e^{-k(t-t_i)}},$$

where $m(t)$ is the body mass (g) at age t (d), A is the asymptotic body mass (g), k is the Gompertz growth constant (d^{-1}), and t_i is the age at the inflection point (d). The relationship between absolute growth rate (G) and body mass at age t was described by a derivative of the Gompertz growth curve:

$$G(t) = -km(t)\ln[m(t)/A].$$

Embryonic growth curves were calculated in accordance with Ricklefs (1987) with the NONLIN procedure of SYSTAT (Wilkinson 1990) as

$$\text{embryonic mass} = [a(1 - b)(t - i)]^{1/(1-b)},$$

where t is day of incubation. Hatchling masses were omitted when fitting the growth curves, because hatchlings were weighed in a fluffy and dry state and their mass included their yolk.

Residuals of RMR, mass, growth rate, and embryonic mass were calculated for the individual chicks as follows: residual value = (measured value − predicted value)/predicted value, where the predicted value of each variable was obtained from its relationship with body mass (for RMR or absolute growth rate) or age (for embryonic mass). To calculate the deviation of hatchling body mass from the embryonic growth curve, the embryonic growth curve was extrapolated to hatching age.

Comparisons were made by Student *t*-tests. Linear regression equations were calculated by the least-square method. ANCOVA was used to test whether the slopes or intercepts of two regression lines differed at the 0.05 significance level (SYSTAT).

Results

Body Mass and Growth Rate

Sexual size dimorphism occurred in all species; males were heavier in turkeys, while females were heavier in guinea fowl and quail. Therefore, Gompertz growth curves were fitted for the sexes separately (Fig. 1). After an initial increase, growth

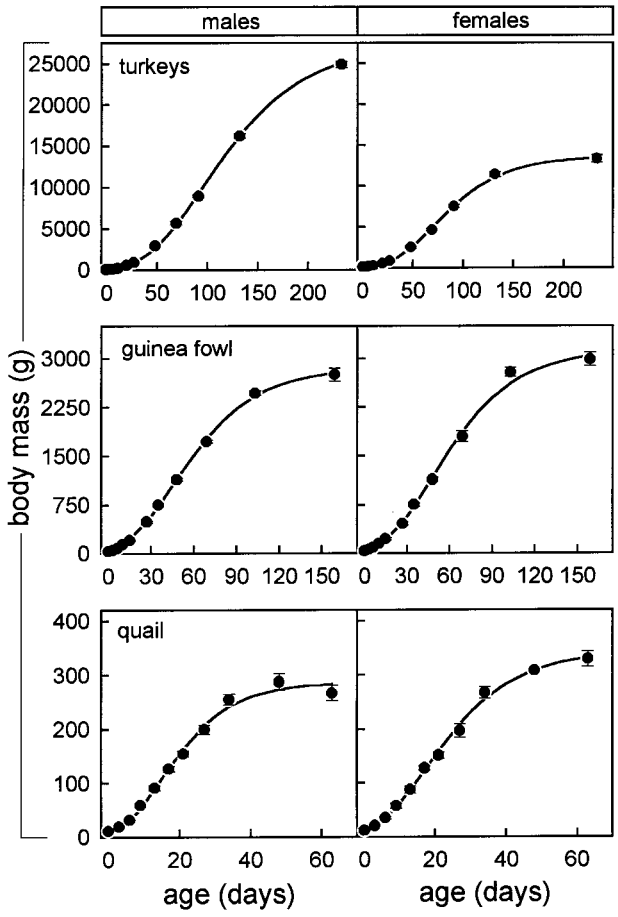

Figure 1. Development of body mass (means ± SEM) with age in male and female chicks of turkey, guinea fowl, and quail. Solid lines represent Gompertz growth curves: turkey males: $Y = 27{,}212\ \exp\{-\exp[-0.018(X - 95.1)]\}$, $N = 118$, $r^2 = 0.995$, $P < 0.01$; turkey females: $Y = 13{,}648\ \exp\{-\exp[-0.025(X - 70.1)]\}$, $N = 68$, $r^2 = 0.989$, $P < 0.01$; guinea fowl males: $Y = 2{,}860\ \exp\{-\exp[-0.031(X - 45.2)]\}$, $N = 100$, $r^2 = 0.990$, $P < 0.01$; guinea fowl females: $Y = 3{,}133\ \exp\{-\exp[-0.031(X - 47.5)]\}$, $N = 82$, $r^2 = 0.988$, $P < 0.01$; quail males: $Y = 286\ \exp\{-\exp[-0.093(X - 14.7)]\}$, $N = 105$, $r^2 = 0.889$, $P < 0.01$; quail females: $Y = 344\ \exp\{-\exp[-0.073(X - 17.4)]\}$, $N = 77$, $r^2 = 0.930$, $P < 0.01$.

rate decreased with body mass (Fig. 2). Embryonic mass increased rapidly in the second half of the incubation period (Fig. 3). In none of the species could a plateau be detected in the development of the embryonic mass, although growth rate decreased slightly toward hatching.

Development of RMR

RMR in the thermoneutral zone increased with body mass in accordance with the general pattern in young precocial birds (Fig. 4). Since RMR did not differ between males and females of equal body mass, we assumed that the developmental patterns did not differ between the sexes, and multiphasic regression models were fitted through the data set as a whole for each species. In turkeys and guinea fowl, a triphasic allometric regression model of RMR fitted the data significantly better than a biphasic allometric regression model (turkeys: $F_{1,\ 183} = 9.51$, $P < 0.01$; guinea fowl: $F_{1,\ 175} = 41.08$, $P < 0.01$). In quail, however, a triphasic pattern did not significantly improve the fit compared with a biphasic model ($F_{1,\ 172} = 2.01$, $P > 0.05$). Breakpoints were found at body masses of about 233 and 6,516 g in turkeys (about 13 and 79 d), 51 and 687 g in guinea fowl (about 3 and 34 d), and 54 g in quail (about 9 d).

Effect of Growth Rate and Accumulated Growth on RMR in Hatchlings

The relationship between the residuals of RMR and growth rate differed between hatchlings and older chicks before the

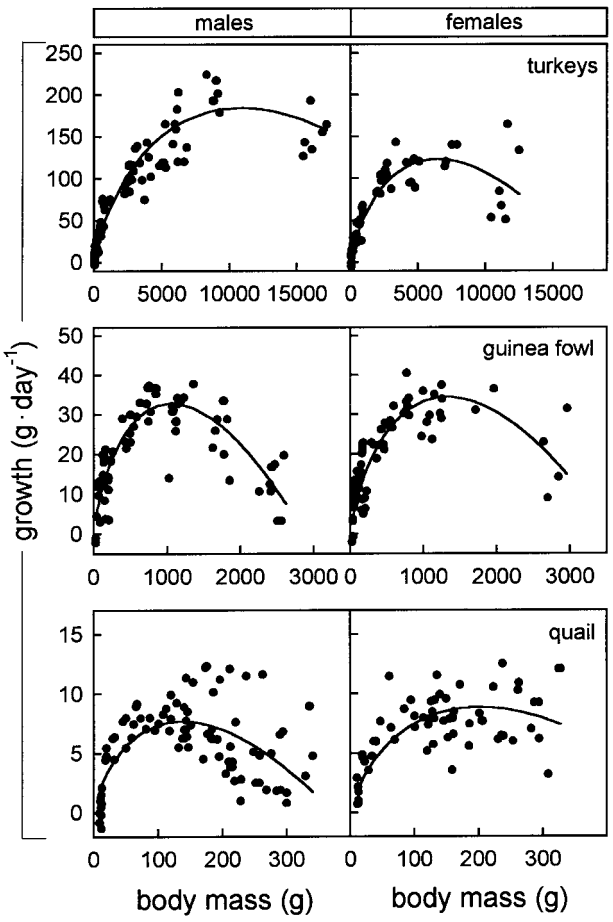

Figure 2. Relationships between absolute growth rate and body mass in male and female chicks of turkey, guinea fowl, and quail. Solid lines represent the following equations: turkey males: $Y = -0.017X \ln(X/29{,}513)$, $N = 108$, $r^2 = 0.922$, $P < 0.01$; turkey females: $Y = -0.019X \ln(X/17{,}575)$, $N = 61$, $r^2 = 0.851$, $P < 0.01$; guinea fowl males: $Y = -0.031X \ln(X/2{,}875)$, $N = 92$, $r^2 = 0.780$, $P < 0.01$; guinea fowl females: $Y = -0.026X \times \ln(X/3{,}595)$, $N = 75$, $r^2 = 0.754$, $P < 0.01$; quail males: $Y = -0.056X \ln(X/373)$, $N = 91$, $r^2 = 0.344$, $P < 0.01$; quail females: $Y = -0.044X \ln(X/547)$, $N = 63$, $r^2 = 0.472$, $P < 0.01$.

first breakpoint (Figs. 5 and 6). In turkey hatchlings, residuals of RMR decreased significantly with residuals of growth rate ($Y = -48.17 - 0.36X$, $N = 13$, $r^2 = 0.561$, $P < 0.01$), while in guinea fowl a negative trend was present although not statistically significant ($Y = -14.64 - 0.31X$, $N = 7$, $r^2 = 0.512$, $P = 0.071$). Thus, hatchlings with relatively low growth rates had relatively high RMRs. In quail, however, no significant relationship or trend was found (Fig. 5).

In none of the species was a significant linear correlation found between the residuals for RMR and embryonic mass (Fig. 5). The residuals in general were negative, because hatchlings were weighed in a dry and fluffy state, while the embryos were weighed wet, and the extrapolated embryonic growth curve overestimated hatchling mass.

In hatchlings, the thermoneutral zone was extremely narrow, and possibly some RMR measurements were obtained at temperatures above or below the actual thermoneutral zone, which might affect the results. The routine body temperature measurements showed that in all species average hatchling body temperature decreased slightly during the 1-h measurement (Table 1). This could result from the exposure to darkness, which caused many very young chicks to fall asleep. The decrease in hatchling body temperature was, however, not significant (paired Student *t*-test, Table 1). Furthermore, no significant linear relationship was found between residuals of RMR and the body temperature after the trial. We presume that the relationships between hatchling residuals of RMR and growth rate or embryonic mass were not affected by body temperature.

Effect of Growth Rate and Accumulated Growth on RMR in Older Chicks

Before the first breakpoint, a positive relationship between residuals of RMR and growth rate was found in turkeys (Fig. 6, left panels; $Y = -5.56 + 0.32X$, $N = 42$, $r^2 = 0.168$, $P < 0.01$) and quail ($Y = -12.03 + 0.42X$, $N = 17$, $r^2 = 0.390$, $P < 0.01$). Both the slopes and intercepts of the regression lines did not differ significantly between turkeys and quail ($F_{1, 55} = 0.202$, $P > 0.5$; $F_{1, 56} = 0.262$, $P > 0.5$, respectively). In turkeys, residuals of RMR were also positively related with residuals of growth rate

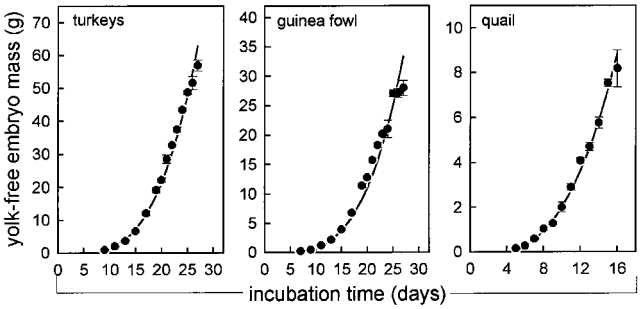

Figure 3. Development of wet, yolk-free embryonic mass (means ± SEM) with incubation time in turkey, guinea fowl, and quail. Solid lines represent the following equations: turkey: $Y = [0.148(X - 2.450)]^{3.215}$, $N = 56$, $r^2 = 0.999$, $P < 0.05$; guinea fowl: $Y = [0.103(X - 0.867)]^{3.559}$, $N = 60$, $r^2 = 0.985$, $P < 0.05$; quail: $Y = [0.159(X - 1.881)]^{2.688}$, $N = 48$, $r^2 = 0.991$, $P < 0.05$.

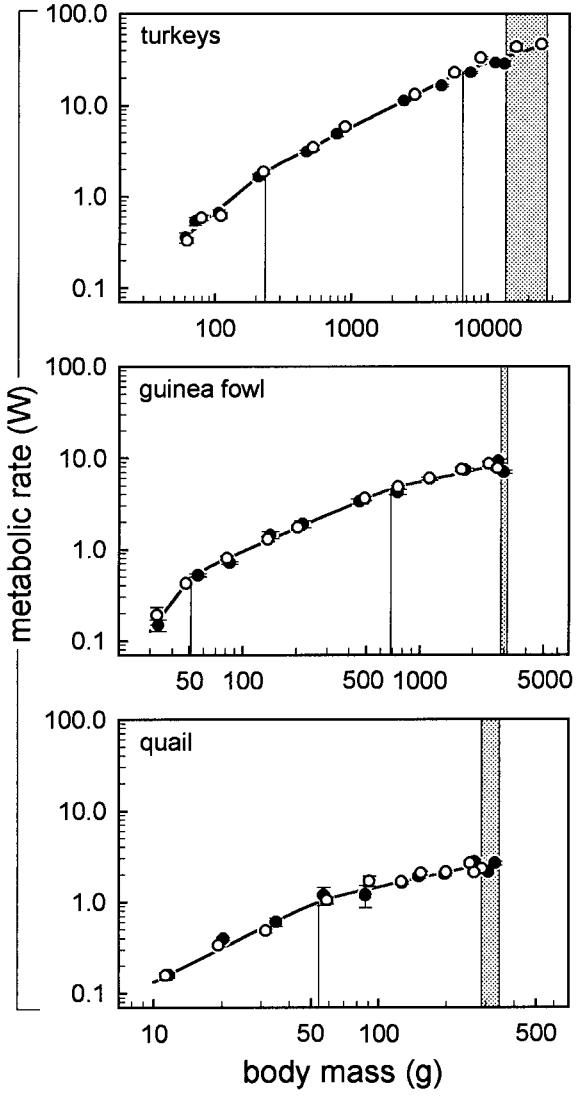

Figure 4. Development of RMR in the thermoneutral zone (means ± SEM) with body mass in turkey, guinea fowl, and quail (*open symbols,* males; *solid symbols,* females). Solid lines represent equations calculated from the general model (see Material and Methods). Parameter values for turkey: $a = -2.646$, $b_1 = 1.239$, $b_2 = 0.754$, $b_3 = 0.483$, $c_1 = 2.367$, $c_2 = 3.814$ ($N = 134$, $r^2 = 0.980$, $P < 0.001$); for guinea fowl: $a = -4.873$, $b_1 = 2.695$, $b_2 = 0.836$, $b_3 = 0.396$, $c_1 = 1.710$, $c_2 = 2.837$ ($N = 181$, $r^2 = 0.979$, $P < 0.001$); and for quail: $a = -2.103$, $b_1 = 1.228$, $b_2 = 0.528$, $c_1 = 1.735$ ($N = 137$, $r^2 = 0.982$, $P < 0.001$). The breakpoints of the bi- and triphasic allometric regressions are indicated by thin lines. Lower and upper boundaries along the *X*-axis of the shaded bars represent female and male asymptotic mass in turkeys, and male and female asymptotic mass in guinea fowl and quail, respectively.

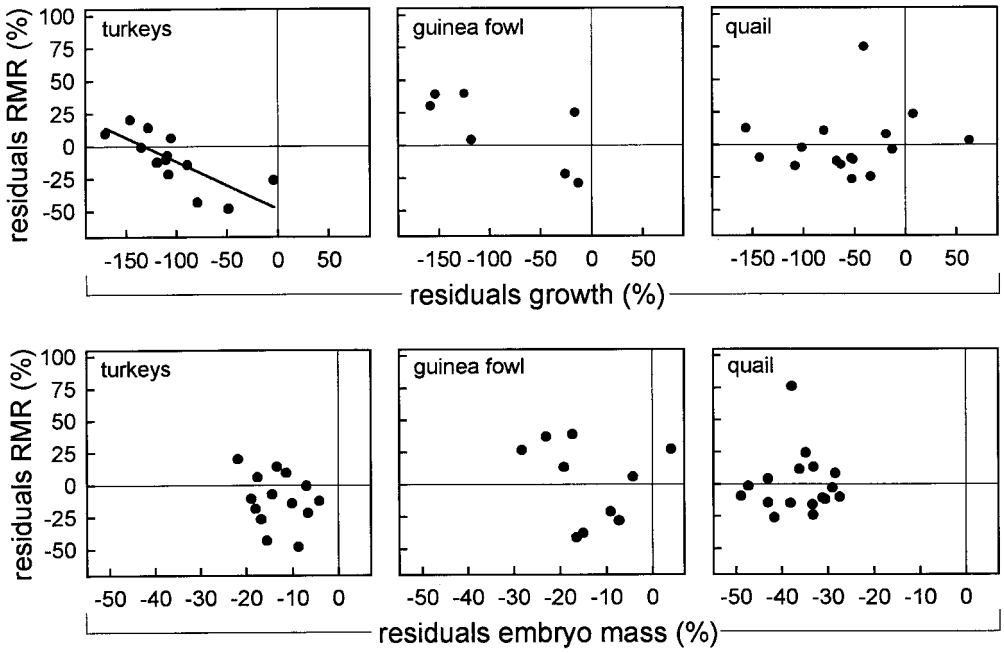

Figure 5. Relationships between the residuals of RMR and absolute growth rate (*top panels*) or embryonic mass (*bottom panels*) in hatchlings of turkey, guinea fowl, and quail. The linear regression equation is given in the text.

in the second phase of the development of RMR (Fig. 6, right panels; $Y = -0.61 + 0.16X$, $N = 89$, $r^2 = 0.118$, $P < 0.01$). Slope and intercept were indistinguishable from those in the first phase ($F_{1, 127} = 2.534$, $P > 0.1$; $F_{1, 128} = 0.543$, $P > 0.1$, respectively). The positive relationships indicate that chicks with relatively high growth rates had relatively high RMRs. In guinea fowl and the other phases in turkey and quail, no significant relationships were found between residuals of RMR and growth rate.

In all species, no significant relationship existed between residuals of RMR and body mass in the first phase of RMR development. In the second phase, a positive relationship was found between residuals of RMR and body mass in guinea fowl (Fig. 7; $Y = 1.54 + 0.32X$, $N = 81$, $r^2 = 0.157$, $P < 0.001$) and quail ($Y = 1.22 + 0.32X$, $N = 144$, $r^2 = 0.076$, $P < 0.01$). This indicates that chicks with relatively high body masses had relatively high RMRs. Both the slopes and intercepts of the regression lines did not differ between guinea fowl and quail ($F_{1, 221} = 0.001$, $P > 0.5$, and $F_{1, 222} = 0.021$, $P > 0.5$, respectively). In turkeys, and in the last phase in guinea fowl, there was no significant correlation between residuals of RMR and body mass.

Discussion

Effect of Growth Rate and Accumulated Growth on RMR in Hatchlings

In none of the species was hatchling RMR correlated with residuals of embryonic mass. This indicates that hatchling maintenance does not simply reflect the growth accumulated during embryonic development. In turkey and guinea fowl hatchlings a negative correlation between residuals of RMR and growth rate was found. Turkey hatchlings in particular are known in the poultry industry for their delay to initiate food uptake. To a lesser extent this applies to guinea fowl as well,

Table 1: Average hatchling body temperature (°C) before (Initial) and after (Final) the RMR measurements

Species	*N*	Initial Body Temperature	Final Body Temperature	*t*	*P*
Turkey	14	40.39 ± .13	40.19 ± .20	.954	.358
Guinea fowl	10	39.76 ± .26	39.20 ± .30	1.318	.220
Quail	17	40.11 ± .18	39.81 ± .23	1.229	.236

Note. Values presented are means ± SD. Also presented are the *t* and *P* values of the paired Student *t*-test between average initial body temperature and final body temperature, and the number of hatchlings (*N*).

while quail hatchlings take their food readily. In turkey, maintenance MR will account for almost all of RMR due to the very low food uptake. When maintenance is high and food uptake very low, hatchlings have to use their internal reserves such as yolk, and this may even induce a decrease in body mass. It seems plausible that the negative correlation between residuals of RMR and growth rate in turkeys and guinea fowl originates from an effect of maintenance MR on growth rate and not the reverse. In quail hatchlings, where food uptake was no problem, a negative correlation would not be expected, and none was found.

In contrast to the negative intraspecific correlation between residuals of RMR and growth rate, the interspecific correlation between hatchling residuals of RMR and average posthatch growth rate is positive in gulls and terns (Klaassen and Drent 1991). This suggests that the physiology of the hatchling is anticipatory, that is, adapted to future growth. Perhaps this positive correlation would be worth looking for in an intraspecific analysis, relating RMR of individual hatchlings to their individual average posthatch growth rates. One should bear in mind that hatchlings should be considered a transition stage between embryonic and posthatching development. Many physiological changes take place during the first 24-h posthatch, for example, the increasing thermogenic ability (Misson

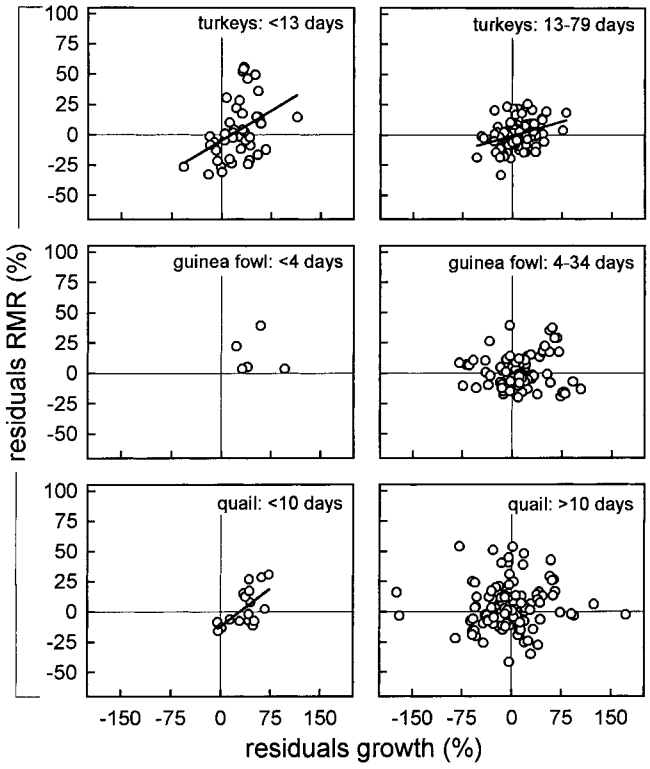

Figure 6. Relationships between the residuals of RMR and absolute growth rate for the first and second phase (*left and right panels,* respectively) in turkey, guinea fowl, and quail. In the third phase, no significant relationships were found. Linear regression equations are given in the text.

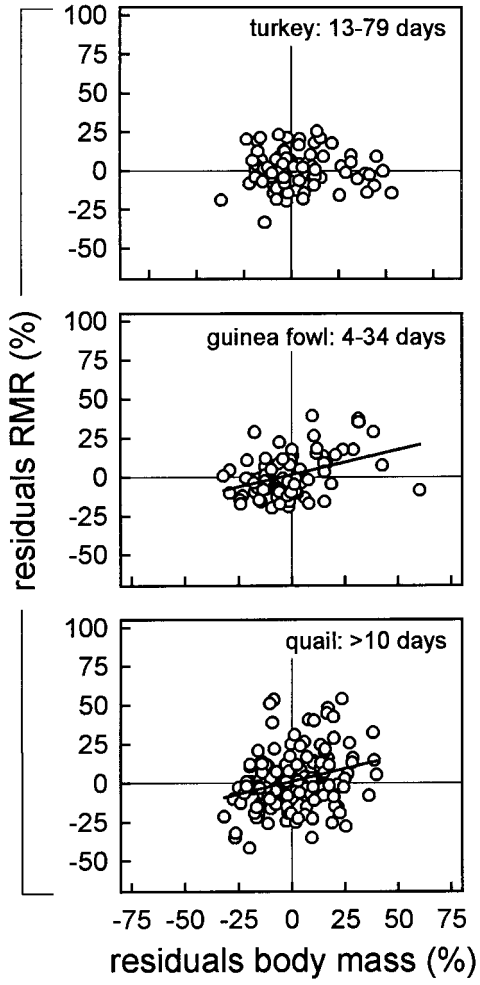

Figure 7. Relationships between the residuals of RMR and body mass for the second phase in turkey, guinea fowl, and quail. In the first and third phase, no significant relationships were found. Linear regression equations are given in the text.

1977; Grav et al. 1988; Dietz and van Kampen 1994). These changes will have a large impact on RMR and may obscure the possible effect of average posthatch growth rate on hatchling RMR in an intraspecific comparison.

Effect of Growth Rate and Accumulated Growth on RMR in Older Chicks

The RMR of chicks includes costs of growth and specific dynamic action. The latter may include some costs of growth, since in large part specific dynamic action is associated with protein synthesis (Janes and Chappell 1995). Growth rate may thus affect gross energy intake and consequently the costs of digestion and biosynthesis, resulting in a positive correlation between RMR and growth rate throughout development. Contrary to this expectation, positive correlations between residuals of RMR and growth rate were not present in guinea fowl, nor in the third phase in turkeys or in the second phase in quail. This suggests that the

positive relationships between residuals of RMR and growth rate found in young turkeys and quail (Fig. 6) were not associated with the momentary effects of growth rate on MR, such as biosynthesis and digestion.

If maintenance metabolism is affected by past growth instead of present growth, we may expect that residuals of RMR and body mass are positively correlated. A problem with this expectation is that MR is also strongly related to body mass itself, because body mass is a measure of the amount of metabolically active tissues. Since the residuals of RMR showed no correlation with body mass, we assume that a correlation between residuals of RMR and body mass indeed reflects the effect of past growth on RMR. In all species, no correlation was found between residuals of RMR and body mass during the first phase. The duration of the first phase is short, and the total absolute body mass increase is small. In this phase, body mass depends heavily on the initial starting mass (i.e., hatchling mass), and variations in residuals of body mass could represent variations in hatchling mass instead of variations in past growth. Furthermore, the residual yolk is absorbed during the first phase, and variations in residuals of body mass could thus also be associated with variations in residual yolk absorption. Both effects may obscure a possible relationship between residuals of RMR and body mass. In the second phase, a positive relationship between residuals of RMR and body mass was present in guinea fowl and quail. The slopes of the regression lines did not differ significantly between the two species and were also indistinguishable from that found in Arctic terns (slope = 0.22, $r^2 = 0.107$; Klaassen and Bech 1992), indicating that the effect of past growth on RMR was comparable between these three species.

The similarity of the slopes of the linear relationships between residuals of RMR and growth or body mass (Table 2) suggests that past and present growth are both linked to maintenance metabolism to the same extent throughout posthatch development. However, other factors are obviously also implicated, since the relationships account for only a modest share of the total variance in residuals of RMR (Table 2). If the coupling between growth and maintenance does not change during development, this could account for the fact that the slope of the interspecific relationship between hatchling RMR and average posthatch growth rate (0.38; Klaassen and Drent 1991) is within the range of the slopes of the intraspecific relationships between RMR and growth found in this study (Table 2). Although we have not measured changes in the size of the metabolically active tissues (such as the liver) during growth, a functional link between RMR and growth rate implies a coupling between relative organ size and hence metabolic contribution to the total RMR, as has been argued for the derivation of adult RMR from organ-specific MR (reviewed by Scott and Evans [1992]). However, metabolic abilities, functional maturity, organ function, and relative size change throughout development (see, e.g., Ricklefs 1983; Grav et al. 1988; Kroghdahl and Sell 1989; Choi et al 1993; Nir et al. 1993; Dietz 1995). Furthermore, the composition of the deposited tissues and thus energy density of deposited tissues changes with age (see, e.g., Ricklefs 1974; Blem 1978; Klaassen 1992; Drent et al. 1992), as well as the growth efficiency (Williams and Prints 1986; Olson 1992). These changes do not follow an invariate pattern but are comparable between species with the same mode of development (Ricklefs 1974, 1983). The many changes that take place during development imply a continuous adjustment of the metabolic machinery to growth processes throughout development, as indicated by the similarity of the slopes of the relationships between RMR and growth. The application of the intraspecific relationship between RMR and growth rate as confirmed in this study necessitate a reevaluation of the classic growth budgets assembled by Ricklefs and White (1981), as is discussed more fully by Weathers (1996). There is a pressing need to extend studies on the ontogeny of RMR in relation to growth rate, although, as we have found, very large samples are called for.

Table 2: Summary of the slopes and r^2 of the linear relationships between residual resting metabolic rate (RMR_{res}), residual growth rate (G_{res}), or residual body mass (m_{res}) for the first and second phase in the development of RMR with body mass in turkey, guinea fowl, and quail

Species	$RMR_{res} \times G_{res}$	$RMR_{res} \times m_{res}$
First phase (excluding day 0):		
Turkey	.32 ± .11; $r^2 = .168$	. . .
Guinea fowl	. . .	. . .
Quail	.42 ± .14; $r^2 = .390$	. . .
Second phase:		
Turkey	.16 ± .05; $r^2 = .118$	. . .
Guinea fowl	. . .	.32 ± .08; $r^2 = .157$
Quail	. . .	.32 ± .10; $r^2 = .076$

Note. In the third phase, no significant linear relationships were present. Slopes are presented ± SEM. Hatchlings were excluded from the analysis.

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